

Species Boundaries of *Sphaerophthalma unicolor* (Hymenoptera: Mutillidae): Is Color Useful for Differentiating Species?

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Abstract.—Taxonomists often use differences in color to diagnose species. This is especially true for velvet ant species (Hymenoptera: Mutillidae), which often are recognized by differences in integumental and setal coloration. Recent molecular analyses have shown that color characteristics are not always useful in distinguishing among mutillid species. Morphological and molecular data are used here to investigate the different color forms of one of the most variable nocturnal velvet ants, the widespread species *Sphaerophthalma unicolor* (Cresson). This analysis also includes some less variable, but closely related species from the *S. unicolor* species-group (Group *rustica sensu* Schuster 1958). Differences were found in genitalic morphology, as well as in the ITS1 and ITS2 rDNA sequences between two distinct color forms. The species boundaries of *S. unicolor* and *S. mendica* (Blake), **new status**, are defined. We report that *Mutilla aspasia* (Blake) and *Photopsis nebulosus* (Blake) are **junior synonyms** of *S. mendica*. Also, the female of *S. angulifera* Schuster is described.

Key words.—Sphaerophthalminae, velvet ant, color characters, species boundaries

Color characters have often been employed by insect taxonomists to differentiate between species. Sometimes, however, using color alone is insufficient to distinguish species due to mimicry complexes (e.g., *Heliconius* butterflies; Sheppard et al. 1985) or highly variable species (e.g., *Dasymutilla quadriguttata* (Say); Pilgrim et al. 2009). Wasps in the family Mutillidae have often been identified largely using differences in setal coloration or integumental pigmentation (Mickel 1924, 1928, 1935, 1936, 1939, 1941, 1943, 1960; Manley 2003; Manley and Pitts 2007; Manley and Williams 2005; Williams and Manley 2006; Pilgrim et al. 2008; Williams and Pitts 2008a). The increased use of molecular tools, particularly the two internal transcribed spacer regions (ITS1 and ITS2), has enabled researchers to determine species boundaries when morphology is ambiguous (Pilgrim and Pitts 2006; Wilson and Pitts 2008; Pitts et al. 2009).

Recent work on the diurnal genera *Dasymutilla* Ashmead and *Pseudomethoca*

Ashmead suggests that increased caution needs to be used when determining whether or not an alternate color form is, indeed, a distinct species. Pilgrim et al. (2008) showed that two species of *Dasymutilla* had been incorrectly described as separate species based, in large part, on the differences in their coloration. Also, Williams and Pitts (2008b) showed that three species of *Pseudomethoca* were improperly classified as one species, largely because they all shared a similar color pattern.

Color has also been used to differentiate between species and subspecies of nocturnal mutillids (e.g. Schuster 1958). Ferguson (1962), however, suggested that pigmentation in sphaerophthalmine mutillids was affected by the temperature and humidity during development. Molecular methods were used to show that the subspecies of the nocturnal mutillid *Dilophotopsis concolor* (Cresson), which were defined principally based on differences in pigmentation, were invalid (Wilson and Pitts 2008).

It is probable, however, that differences in color do sometimes reflect species-level differences among members of the family Mutillidae. For example, *Dasymutilla asteria* Mickel and *D. sicheliana* (Saussure) are molecularly distinct, yet are nearly identical structurally. These species, however, can be recognized based on differences in setal coloration. Also, the nocturnal species in the *S. imperialis* species-group, such as *Sphaerophthalma marpesia* (Blake) and *S. megagnathos* Schuster, can be identified by differences in their color patterns (Pitts 2006).

Sphaerophthalma unicolor (Cresson) is a common, wide-ranging nocturnal mutillid. The specific epithet given to this wasp is unfortunate, because this species is polymorphic in both setal coloration and cuticular pigmentation. Males exhibit three distinct color forms: some specimens have a reddish-black integument with yellowish wings; others have a reddish-brown integument with clear wings and white pubescence on the metasoma; and, lastly, there are others with yellowish-brown integument, clear wings and orange pubescence on the metasoma. Females also are found in two main color forms: some are covered with setae ranging from red to yellow, while the others have distinct white setae on the fringes of the metasomal segments. The extreme variability in the coloration of this wasp has led to numerous synonyms being described, largely based on differences in coloration. Ferguson (1967) synonymized nine names with *S. unicolor* based on the study of over 1,000 specimens. Interestingly, he insinuated that the difference in coloration of the forms is linked to elevation, stating that the Melanistic-color form was only found in higher elevations across the Great Basin and Mojave Deserts, while the Reddish-brown color form was present only in the lower elevations (Ferguson 1967). The allopatry observed by Ferguson (1967) in the two distinct color forms suggests elevation could be a barrier to gene flow, and that

these two forms may represent distinct species.

This paper reports on molecular and morphological examinations that test the species boundaries of *S. unicolor*. The species-specific loci 1st and 2nd internal transcribed spacer regions (ITS1 and ITS2) and morphology are used to determine if the different color forms of *S. unicolor* represent distinct species by comparing genetic distances between color forms, and related species.

In the course of this study, the female of a closely related species, *S. angulifera* Schuster, was found. We described the female here and compared it to that of *S. unicolor*.

MATERIALS AND METHODS

Sampling

Specimens were collected from sites across western North America from 2002 to 2007 using black light traps, fluorescent lantern traps, and by hand. All specimens were placed directly into 95% ethanol and those used for molecular examination have been labeled as voucher specimens and deposited in the Department of Biology Insect Collection, Utah State University, Logan, UT (EMUS). All holotypes were examined and compared to molecular voucher specimens. An attempt was made to sample *S. unicolor* from all parts of its range and from each of its different color forms.

Three outgroups, *Sphaerophthalma angulifera*, *S. pinalea* Schuster and *S. triangularis* (Blake), were included in the analysis, because they are closely related to *S. unicolor* (Schuster 1958; Pitts unpub. data). Although Schuster (1958) included four other species in the *S. unicolor* species-group, we did not include *S. pluto* (Fox) or *S. juxta* (Blake) because they are so genetically different from the other members of the species-group that they obviously do not belong in the group. We were also

unable to include *S. tetricuspis* Schuster and *S. subtriangularis* Schuster, because they are found in Baja California and no fresh specimens were available from this area for molecular analysis.

Morphological analysis

All specimens were examined with a Wild M-5 stereo microscope and all measurements were made with an ocular micrometer. Eye size of females was determined by measuring the maximum longitudinal length of the eye compared to the length from the posterior margin of the eye to the vertex of the head. Eye length is reported as a ratio of the eye length to the eye-to-vertex length. Specimens were borrowed from or deposited into the following collections:

ANSP	Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
BYUC	Entomology Section, Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA.
CISC	Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, California, USA.
CSCA	California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California, USA.
EMUS	Department of Biology Insect Collection, Utah State University, Logan, Utah, USA.
LACM	Insect Collection, Los Angeles County Museum of Natural History, Los Angeles, California, USA.
NVDA	Nevada State Department of Agriculture, Reno, Nevada, USA.
PMNH	Peabody Museum of Natural History, Yale University, New Haven Connecticut, USA.

UCDC	The Bohart Museum of Entomology, University of California, Davis, California, USA.
UCRC	UCR Entomological Teaching and Research Collection, University of California, Riverside, California, USA.
UMSP	University of Minnesota Insect Collection, St. Paul, Minnesota, USA.
USNM	United States National Entomological Collection, Department of Entomology, U.S. National Museum of Natural History, Washington D.C., USA.

Molecular analysis

DNA was extracted, amplified, and sequenced from individuals from each of the three color forms of *S. unicolor*, as well as some related species. DNA extraction and amplification of the two rDNA internal transcribed spacer regions (ITS1 and ITS2) followed the protocols outlined by Pilgrim and Pitts (2006). Sequences were analyzed with an ABI Prism 377, 3100, or 3730 Genetic Analyzer. All PCR products were sequenced in both directions and were combined in Sequencher 4.1 (Gene Code Corp., Ann Arbor, MI). Pair-wise percent genetic distances between subspecies were calculated by determining the number of differences (point mutations and insertions or deletions) and dividing by the number of base pairs of the longer of the two sequences. Gel electrophoresis of each gene yielded a single band for each individual wasp and the resulting DNA was sequenced cleanly suggesting no gene heterogeneity as seen in some other organisms (e.g., Harris and Crandall 2000; Parkin and Butlin 2004; Bower et al. 2008).

Phylogenetic analysis

The two genetic loci were subjected to Bayesian analysis using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Sequences were analyzed as a combined data

set, with each gene partitioned according to the general time-reversible model (Lanave et al. 1984) with invariant sites and gamma-distributed rate variation across sites (GTR+I+ Γ) and with all parameters unlinked across loci. Bayesian analyses included four independent runs with three heated chains and one cold chain in each run. The MCMC chains were set for 3,000,000 generations and sampled every 100 generations; chains were run until the average standard deviation of the split frequencies dropped below 0.01. The burn-in period for each analysis was removed after graphical determination of stationarity.

RESULTS

Molecular Results

Genetic distances were low between individuals exhibiting the color form defined by having yellowish-brown integument, clear wings and orange pubescence on the metasoma (0% for ITS1 and 0.2% for ITS2: Table 1). Four of the five individuals exhibiting this color form had identical ITS1 and ITS2 sequences, so only one of these genetically identical individuals is included in Table 1. Genetic distances were also low among the form characterized by reddish-brown integument with clear wings and white pubescence on the metasoma (0.3% for ITS1 and 0.7% for ITS2: Table 1). The genetic distances were similar between the melanistic individuals (0.3% for ITS1 and 0.4% for ITS2: Table 1). Genetic distances were also relatively low between the Melanistic form and the Reddish-brown form with white pubescence (0.6%–1.10% for ITS1 and 0.5%–0.9% for ITS2: Table 1). The genetic distance between both forms with white pubescence and the form with orange pubescence was high (1.4%–1.7% for ITS1 and 1.9%–2.5% for ITS2: Table 1). These distances are as great as or greater than the genetic distance between any of the *S. unicolor* forms and the closely related species *S. angulifera*

(0.9%–2.6% for ITS1 and 1.2%–2.5% for ITS2: Table 1). All sequences have been submitted to GenBank (Accession nos. GQ182985–GQ183013: Table 2).

Phylogenetic Results

Bayesian analysis of the combined molecular data produced a tree that clearly depicts the relationships among the color variants of *S. unicolor* and the outgroups (Fig. 1). This topology revealed three distinct clades that are separated from the outgroups by a relatively long branch length (large genetic distance). One clade is made up of *S. unicolor* specimens that have white pubescence on the metasoma, another is composed of *S. unicolor* specimens with orange pubescence on the metasoma, and the last clade is made up of *S. angulifera* specimens (Fig. 1). The relationships among these three clades are unclear, yet the distinctness of each is supported by a large posterior probability (1.0). While there was a separation between individuals with a reddish-black integument and those with a reddish-brown integument, the branch length separating these groups was small.

Morphological Results

Careful examination of numerous *S. unicolor* specimens revealed consistent morphological differences between the color form with dense fringes of orange setae on the margins of the tergites and the color form with dense fringes of white setae on the tergites. No consistent differences, besides integumental coloration, were found between the Reddish-brown form and the Reddish-black form. Among males, differences were found in the length and shape of the cuspis on the genitalia (Figs 2–5), as well as differences in setal coloration. Among females, differences were found in the size of the eyes, pygidial sculpture, as well as differences in setal coloration. While there were differences in integumental coloration in some of the male specimens, some had a reddish-black

Table 1. Genetic differences among the *Sphaerophthalma* species belonging to the *unicolor* species-group (ITS1 above diagonal, and ITS2 below).

	ITS1											
	<i>S. mendica</i>	<i>S. mendica</i>	<i>S. mendica</i>	<i>S. mendica</i> (melanistic)	<i>S. mendica</i> (melanistic)	<i>S. mendica</i> (melanistic)	<i>S. unicolor</i>	<i>S. unicolor</i>	<i>S. angulifera</i>	<i>S. angulifera</i>	<i>S. pinalea</i>	<i>S. triangularis</i>
<i>S. mendica</i>	-	0.6%	0.3%	0.9%	1.2%	0.9%	1.8%	1.8%	2.7%	2.7%	9.0%	9.0%
<i>S. mendica</i>	0.3%	-	0.3%	0.9%	1.2%	0.9%	1.8%	1.8%	2.7%	2.7%	9.0%	9.0%
<i>S. mendica</i>	0.5%	0.8%	-	0.6%	0.9%	0.6%	1.5%	1.5%	2.4%	2.4%	8.6%	8.6%
<i>S. mendica</i> (melanistic)	0.4%	0.6%	0.6%	-	0.3%	0.0%	1.5%	1.5%	2.4%	2.4%	8.6%	8.6%
<i>S. mendica</i> (melanistic)	0.3%	0.5%	0.5%	0.4%	-	0.3%	1.8%	1.8%	2.7%	2.7%	8.6%	8.6%
<i>S. mendica</i> (melanistic)	0.3%	0.5%	0.5%	0.4%	0.3%	-	1.5%	1.5%	2.4%	2.4%	8.6%	8.6%
<i>S. unicolor</i>	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	0.0%	0.0%	0.9%	0.9%	7.6%	7.6%
<i>S. unicolor</i>	1.8%	2.1%	2.1%	2.0%	1.8%	1.8%	-	0.3%	0.9%	0.9%	7.6%	7.6%
<i>S. unicolor</i>	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	0.3%	0.0%	0.9%	0.9%	7.6%	7.6%
<i>S. unicolor</i>	1.6%	1.8%	1.8%	1.7%	1.6%	1.6%	0.0%	0.0%	0.9%	0.9%	7.6%	7.6%
<i>S. angulifera</i>	1.3%	1.6%	1.6%	1.4%	1.3%	1.3%	2.1%	2.4%	-	0.6%	7.3%	7.9%
<i>S. angulifera</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	-	7.9%	7.9%
<i>S. pinalea</i>	8.8%	9.1%	9.0%	8.9%	8.5%	8.8%	9.0%	9.3%	8.9%	NA	-	3.0%
<i>S. triangularis</i>	9.0%	9.3%	9.3%	8.9%	9.0%	9.0%	9.3%	9.6%	9.1%	NA	5.6%	-

ITS2

Table 2. Genbank Accession numbers and descriptive information about the velvet ant specimens used in the genetic analyses.

Species	Voucher ID	Collection Location	ITS1 Accession #	ITS2 Accession #
<i>S. angulifera</i>	JP276	CA, San Bernardino Co., 5.5 mi S Barstow	GQ182985	GQ183000
<i>S. angulifera</i>	JW04	UT, Washington Co., 3 mi West of Bloomington	GQ182986	NA
<i>S. mendica</i>	JP555	NV, Nye Co., Pahrump	GQ182990	GQ183004
<i>S. mendica</i>	JP556	UT, Garfield Co., Alvey Wash, 5 km S Escalante	GQ182991	GQ183005
<i>S. mendica</i>	JP625	UT, San Juan Co., Valley of the Gods	GQ182994	GQ183008
<i>S. mendica</i>	JP626	NM, San Juan Co., 3 mi S Farmington	GQ182995	GQ183009
<i>S. mendica</i>	JW12	UT, Garfield Co., Alvey Wash, 7 km S Escalante	GQ182998	GQ183012
<i>S. mendica</i>	KW08	CA, Riverside Co., Corn Springs	GQ182999	GQ183013
<i>S. pinalea</i>	JP761	AZ, Cochise Co., Carr Canyon	GQ182987	GQ183001
<i>S. triangularis</i>	JP108	AZ, Cochise Co., San Pedro Riparian Cons. Area	GQ182988	GQ183002
<i>S. unicolor</i>	JP102	CA, Riverside Co., Bautista Canyon	GQ182989	GQ183003
<i>S. unicolor</i>	JP557	CA, Kern Co., 10 mi WSW McKittrick	GQ182992	GQ183006
<i>S. unicolor</i>	JP558	CA, Solano Co., Stebbins Cold Canyon Reservoir	GQ182993	GQ183007
<i>S. unicolor</i>	JP712	CA, Solano Co., Suisun City, Rush Ranch	GQ182996	GQ183010
<i>S. unicolor</i>	JP97	CA, Riverside Co., Bautista Canyon	GQ182997	GQ183011

integument while others had reddish-brown, no differences in genitalia morphology were found.

An examination of *S. angulifera* revealed similar genitalic morphology to the color form of *S. unicolor* with dense fringes of orange setae on the margins of the tergites (Figs 2–5). Also, the mandibles of *S. angulifera* are different from those of any of the color forms of *S. unicolor*, with the base of the mandibles being wide, the dorsal carina terminating at ½ the distance from the base forming a lobe, and the presence of a small angulate ventral tooth.

Based on the above molecular and morphological data, we are recognizing *S. unicolor* and *S. mendica* as distinct species in the following taxonomic section.

Sphaerophthalma unicolor (Cresson)

Mutilla unicolor Cresson, 1865. Ent. Soc. Phila., Proc. 4: 389. Male. Lectotype data: California, type no. 1887 (ANSP).

Mutilla auraria Blake, 1879. Amer. Ent. Soc., Trans. 7: 248. Female. Holotype data: Nevada, type no. 4573 (ANSP).

Mutilla phaedra Blake, 1879. Amer. Ent. Soc., Trans. 7: 251. Female. Holotype data: Nevada, type no. 4575 (ANSP).

Agama rustica Blake, 1879. Amer. Ent. Soc., Trans. 7: 252. Male. Holotype data: California, type no. 4550 (ANSP).

Photopsis nebulosus Blake, 1886. Amer. Ent. Soc., Trans. 13: 275. Male. Holotype data: Nevada, type no. 4549 (ANSP).

Sphaerophthalmia (*sic.*) *anthophora* Ashmead, 1897. In: Davidson, South. Calif. Acad. Sci. Proc. 1: 5. Male Holotype data: California, Los Angeles, type no. 6113; Female Allotype data: California, Los Angeles, type no. 6113 (USNM).

Mutilla monochroa Dalle Torre, 1897. Cat. Hymen. 8: 63. New name for *M. unicolor* Cresson.

Dasymutilla sumneriella Cockerell, 1915. Entomologist 48: 259. Female. Holotype data: California, La Jolla, type no. 20409 (USNM)

Sphaerophthalma (*Photopsis*) *rustica ocellaria* Schuster, 1958. Ent. Amer. 37: 32. Male. Holotype data: California, Berkeley (UMSP).

Diagnosis of male.—The male of this species can be recognized by having mandibles that are weakly excised ventral-ly with an indistinct basal tooth and an

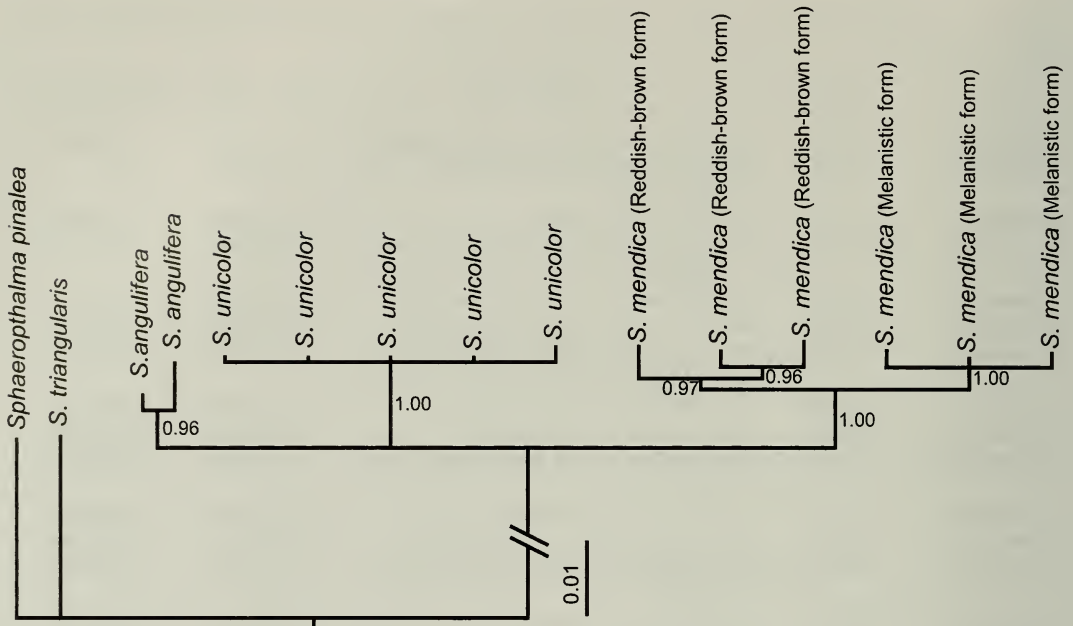


Fig. 1. Consensus tree of Bayesian analysis of the combined ITS1 and ITS2 sequences. Numbers at each branch represent posterior probabilities. Because a long branch separates the outgroup taxa from the ingroup taxa, we shortened this branch length; the genetic distance between the outgroup taxa and the ingroup taxa can be found in Table 1.

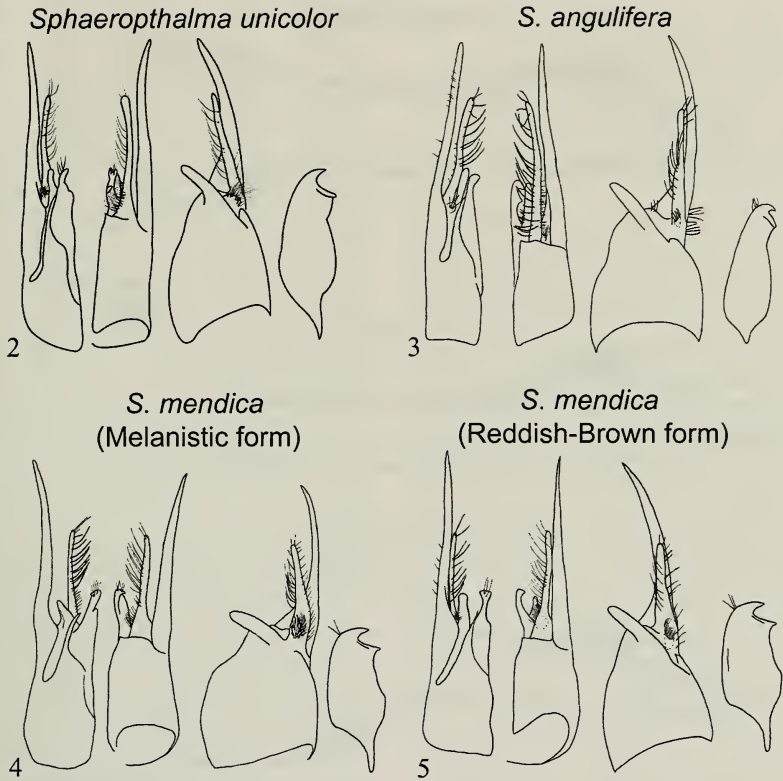
apex that is tridentate and oblique (Fig. 6), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia are similar to *S. triangularis*, but the cuspis is only approximately 3/4 the free length of the paramere, rather than almost as long as the paramere (Fig. 2). The cuspis is a uniform diameter from the base to the apex (Fig. 2). This species has the apical margins of the tergites with dense fringes of orange plumose setae and often orange setae covering the head and mesosoma.

Diagnosis of female.—The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with dense erect red to pale orange brachyplumose setae that obscure the integument; the ventral margin of the mandible has a slight excision, but lacks a ventral tooth; the head below the eyes widens towards the mandibular insertions; the first metasoma segment is

sessile with the second segment; and the pygidium is longitudinally striate and granulate between the striae; the eye length is less than the length from the posterior margin of the eye to the vertex of the head (the eye is from 0.85 to 0.92 times as big as the length from the margin of the eye to the vertex of the head); and the apical margins of the tergites have dense fringes of orange plumose setae. Often, orange setae are covering the head and mesosoma as well.

Distribution.—This species is common in the Central Valley of California and west of the Southern California Coastal Mountain Ranges. It is also present at the extreme western margin of the Great Basin Desert, along the foothills of the eastern side of the Sierra Nevada Range.

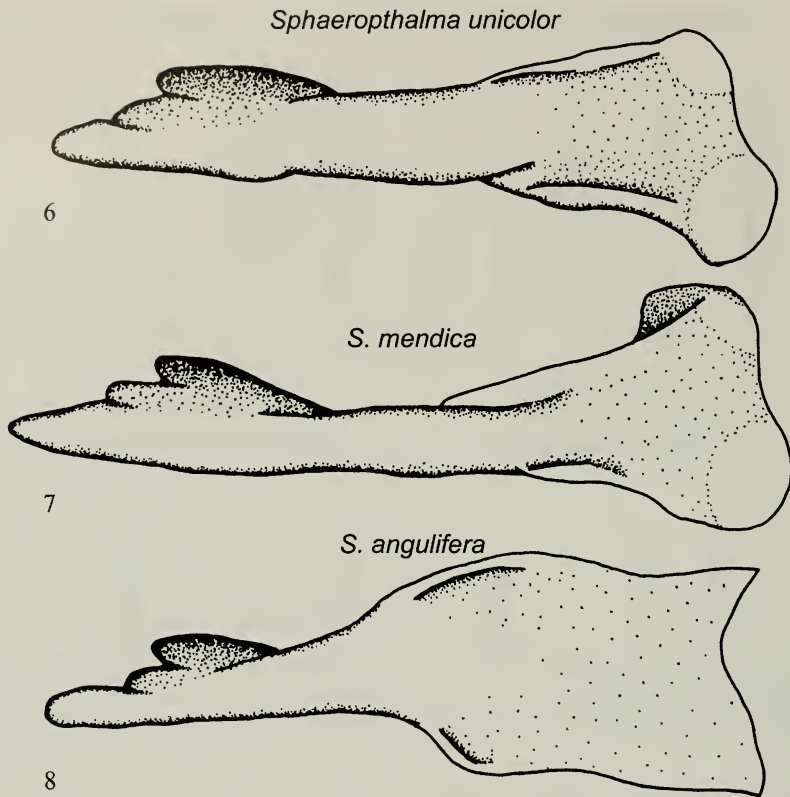
Material examined.—**MEXICO:** Baja California: Rancho sonora bampo, 54 mi S Tijuana, 3 ♂, 16.May.1959, J.A. Honey (LACM). **USA:** California: Colusa Co.: Colusa, 3 ♂, 15.Aug.1955, R. Schuster (UCDC); Fresno Co.: Fresno, 1 ♂, 28.May.1956, 2 ♂, 3.Jun.1956, Schuster (UCDC); Helm, 1 ♂, 26.Jul.1960, R.R. Snelling (LACM);



Figs 2–5. Genitalia: dorsal view left; ventral view right; internal lateral view, penial valve removed; penial valve, lateral view; 2. *Sphaerophthalma unicolor*; 3. *S. angulifera*; 4. *S. mendica* (Melanistic color form); and 5. *S. mendica* (Reddish-brown color form).

Little Panoche Reservoir, 4 mi W of I-5, 6 ♂, 27.May.2005, E.E. and K.A. Williams (KAWC); Parkfield, 2 ♂, 28.Sep.1968, E.A. Kane (LACM); Lake Co.: Soda Bay, 1 ♂, 17.Jul.1959, 4 ♂, 25.Jul.1958, R.E. Dolphin (UCDC); Los Angeles Co.: Big Rock Creek, San Gabriel Mts, 1 ♂, .Oct.1959, Honey and Sphon (LACM); Boquet Cyn, 1 ♂, 28.Jul.1938, 1 ♂, 23.Jul.1937, N. Westerland (LACM); Claremont, 1 ♀ (EMUS); Glendale, 1 ♂, 21.Jun.1951, W.M. Schlinger, 1 ♂, 11.Jul.1952, 1 ♂, 25.Aug.1954, 1 ♂, 29.Aug.1951, 1 ♂, Aug.1953, 1 ♂, 11.Sep.1949, 1 ♂, 10.Oct.1951, E.I. Schlinger (UCDC); 1 ♂, 1952, W.M. Schlinger (EMUS); Laurel Cyn, 1 ♂, 28.Jul.1968, B. Duff (LACM); Malibu, 1 ♀, 3.Jul.1950, D.R. Estes (EMUS); San Dimas, 1 ♂, 1953 (LACM); San Gab Cyn, 1 ♂, 10.Jul.1965 (LACM); Tanbark Flat, San Gabriel Mts, 10 ♂, 7.Jul.1963, R.R. Snelling (LACM); Tanbark Flat, 15 ♂, 38 ♀, 21–25.Jun.1956, 1 ♂, 25.Jun.1956, A. Menke Jr., 1 ♂, 1.Jul.1950, J.D. Paschke, 1 ♂, 3.Jul.1950, H.L. Hansen, 2 ♂, 17.Jul.1956, R.G. Bechtel, 1 ♂,

17.Jul.1959, P.D. Hurd, 2 ♂, 19.Aug.1950, E.B. Goodwin, 3 ♂, 20.Aug.1950, E.B. Goodwin, 4 ♂, 2–3.Sep.1950, E.B. Goodwin, 2 ♂, 14.Sep.1950, E.B. Goodwin (UCDC); Kern Co.: Bakersfield, 1 ♂, 11.Jun.1968, E.A. Kane, 1 ♂, 11.Jul.1951, 1 ♂, 14.Jul.1951, 2 ♂, 18.Jul.1951, 1 ♂, 27.Jul.1951, I.W. Isaak (LACM); Maricopa, 22 mi S, Valle Vista Cpgrd., 5 ♂, 16.Sep.2004, E.E. and K.A. Williams (KAWC); Wasco, 26 ♂, 26.Jun.1951, 1 ♂, 27.Jun.1951, 1 ♂, 9.Jul.1951, L.W. Isaak (UCDC); Woody, 1 ♂, 15.Jul.1951, L.W. Isaak (UCDC); Marin Co.: Mill Valley, Lee Street, 2 ♂ 5–6.Aug.1966, 1 ♂, 30.Sep.1966, T.W. Davies (PMNH); Merced Co.: Livingston, 1 ♂, 30.Sep.1961, R. Howkswarth (LACM); Monterey Co.: San Ardo, 2 ♂, 24.Jul.1969, R.E. Doty (LACM); Plumas Co.: Greenville, 1 ♂, 11.Jul.1959, L.A. Stange (UCDC); Riverside Co.: Garner Valley, Kenworthy forest service station on Morris ranch rd., 2 ♂, 4.Jun.2002, M.E. Irwin and F.D. Parker (EMUS); Menifee Valley, hills on W end, 1 ♂, 23.Jul.1981, J.D. Pinto (UCRC);



Figs 6–8. Mandibles: 6. *Sphaerophthalma unicolor*; 7. *S. mendica*; and 8. *S. angulifera*.

San Timeteo Cyn, 4 ♂, 24–25.Sep.1969, M. Feigen and R. Hardy (LACM); The Gavilan, 1 ♂, 17.May.1951, E.L. Schlinger, R.G. Bechtel and E.J. Tayler (UCDC); UC Riverside, 1 ♂, 8–15.Oct.1979, J. Lasalle (UCRC); Winchester, 1 ♂, 5.Sep.1967, W. Icenogle (LACM); *San Bernardino Co.*: Camp O-ongo, nr running spr, San Bernardino Mtns, 2 ♂, 8–12.Aug.1966, C.L. Hogue (LACM); Meyer Can Rd, 5 mi NW Beuore, 5 ♀, 24–27.Sep.1975, M. Wasbauer (CSCA); *San Diego Co.*: dodge Valley, 1 ♂, 26.Mar.1958, E.I. Schlinger (UCDC); El Cajon, 4 mi S, 1 ♀, 27.Apr.1964, R. Ballard (EMUS); Rancho Santa Fé, 3 ♂, 4.Oct.1958, J. Northern (LACM); Scissors xing, 5.5 mi NW, 1 ♂, 8.Jul.1969, A.R. Hardy (LACM); *San Luis Obispo Co.*: Shandon, 1 ♂, 17.Sep.1968 (LACM); *Sacramento Co.*: Rio Linda, 3 ♂, 11.Jul.1959, J. Fowler (UCDC); *Santa Barbara Co.*: Painted Cave, 1 ♂, 7.Aug.1964, C.L. Remington (PMNH); Santa Cruz Island: UC reserve station, Cañada del Medio, 2 ♂, 30–31.Jul.1970, 1 ♂, 14.Aug.1968, 2 ♂, 19–29.Aug.1974, 1 ♂, 25–26.Aug.1971, 1 ♂, 10.Oct.1972, C.L. Remington (PMNH); Beecher's

Bay, 1 ♂, 3–5.Oct.1972, L. Laughrin (PMNH); Toro Canyon Park, 1 ♂, 5–11.Oct.1999, R.L. Doult (EMUS); *Shasta Co.*: Anderson, 2 ♂, Jul–Aug.1955, J. Willis (UCDC); Hat Creek, 1 ♂, 15.Jul.1955, Hogue (LACM), 1 ♂, 10.Jul.1955, 2 ♂, 16.Jul.1955, R.D. Browning, 1 ♂, 14.Jul.1955, E.I. Schlinger (UCDC); *Siskiyou Co.*: Weed, 5 mi SW, 3 ♂, 4 ♀, 9.Jun.2004, K.A. Williams (KAWC); *Sonoma Co.*: Mirabel Park, 1 ♂, 9–18.Aug.1962, C. Slobodchikoff (CISC); *Stanislaus Co.*: Del Puerto Cyn, 1 ♂, 13.Sep.2003, E.E. and K.A. Williams (KAWC); Stanislaus University, 2 ♂, 21.Oct.1905 (EMUS, LACM); *Tehama Co.*: Los Molinos, 1 ♂, 20.Jul.1956, 1 ♂ 24.Jul.1956, E. Yeomanr (UCDC); *Tuolumne Co.*: Strawberry, 1 ♂, 30.Jun.1951, C.A. Downing (UCDC); *Ventura Co.*: Anacapa Island, 2 ♂, 18.Aug.1940, C. Henne, 1 ♂, 23.Aug.1949, G.P. Kanakoff (LACM); *Yolo Co.*: Dunningan, 3.5 mi NW, 3 ♂, 17.Jun.1959, J. Fowler (UCDC); 4 mi SW, 1 ♂, 14.Jul.1959, 3 ♂, 28.Jul.1959, 1 ♂, 31.Jul.1959, 1 ♂, 4.Aug.1959, 1 ♂, 11.Aug.1959, J. Fowler (UCDC); 7 mi NW, 1 ♂, 15.May.1959, 3 ♂, 1.Jul.1959, 15 ♂, 12.Jul.1959, 5 ♂, 14.Jul.1959, 1 ♂, 15.Jul.1959, 5 ♂, 16.Jul.1959, 2 ♂, 21.Jul.1959, 2

♂, 22.Jul.1959, 2 ♂ 23.Jul.1959, 1 ♂, 28.Aug.1959, 3 ♂, 2.Sep.1959, 1 ♂, 29.Sep.1959, J. Fowler (UCDC); Rumsey, 1 ♂, 23.Jul.1955, 1 ♂, 5.aug.1955, E.A. Kurtis (UCDC); Winters, 8 mi NW, 1 ♂, 5.Jun.1959, 3 ♂, 22.Jun.1959, 3 ♂, 25.Jun.1959, 1 ♂, 1.Jul.1959, 1 ♂, 8.Jul.1959, 2 ♂, 13.Jul.1959, 1 ♂, 16.Jul.1959, 1 ♂, 5.Aug.1959, 1 ♂, 11.Aug.1959, 1 ♂, 28.Aug.1959, 4 ♂, 2.Sep.1959, J. Fowler (UCDC); Yolo, 3 mi NW, 1 ♂, 1.Jul.1959, J. Fowler (UCDC); Zamora, 9 mi W, 1 ♂, 28.Jul.1959, 1 ♂, 11.Aug.1959, J. Fowler (UCDC); Yuba Co.: Wheatland, 5 mi N, 1 ♂, 11.Sep.2000, B.L. Williams (KAWC). Nevada, Carson City: Carson City, Ash Cyn, 1 ♂, May–Sep.1981, J.B. Knight (NVDA); Washoe Co.: Thomas Creek, 1 ♂, 3.Aug.1972 (NVDA); Reno, 1 ♂, 5.Jun.1979, 1 ♂, 11.Jun.1979, R.C. Bechtel (NVDA); Washoe Lake State Park, 16 mi S Reno, 1 ♂, 1 ♀, 2.Aug.2005, K.A. Williams (KAWC). Oregon, Grant Co.: John Day, 1 ♀, 8.Oct.1971, O. Warger (PMNH). Washington, Benton Co.: Hanford Site, 1 ♂, 1.Sep.1995, R.S. Zack (EMUS); Klickitat Co.: Pot Hole lake, 1 ♀, 15.Jul.1963, D. Mays (PMNH)

Remarks.—While morphologically similar to *S. mendica*, *S. unicolor* can be easily recognized by color. The integument of *S. unicolor* is generally lighter than *S. mendica* and the setae are orange on the fringes of the tergites rather than white. In older specimens, the orange setae have often faded to a pale yellow, but are not white like the setae of *S. mendica*. The differences in color between these two species are consistent, yet there is some color variation among *S. unicolor* individuals. We have examined some individuals from the Central Valley of California that have a dark melanistic integument similar to some of the *S. mendica* specimens. However, these melanistic *S. unicolor* individuals retained the distinct setal coloration characteristic of the species. Female *S. unicolor* specimens range from having orange to dark red setae, which may explain why they have been confused for *Dasytutilla*.

Sphaerophthalma mendica (Blake), NEW STATUS

Agama mendica Blake, 1871. Amer. Ent. Soc., Trans. 3: 259. Male. Holotype data: Nevada, type no. 4551 (ANSP).

Mutilla aspasia Blake, 1879. Amer. Ent. Soc., Trans. 7: 250. Female. Holotype data: Nevada, type no. 4574 (ANSP). **New Synonym.**

Photopsis nebulosus Blake, 1886. Amer. Ent. Soc., Trans. 13: 275. Male. Holotype data: Nevada, type no. 4549 (ANSP). **New Synonym.**

Diagnosis of male.—The male of this species can be recognized by having mandibles that are weakly excised ventrally with an indistinct basal tooth and an apex that is tridentate and oblique (Fig. 7), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia are similar to *S. unicolor*, but the cuspis is approximately half the length of the parameres (Figs 4–5). The cuspis is nearly twice the diameter at the base compared to the diameter at the apex (Figs 4–5). This species has the apical margins of the tergites with dense fringes of white plumose setae and often white to orange setae covering the head and mesosoma.

Diagnosis of female.—The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with dense erect red to pale orange brachyplumose setae that obscure the integument; the ventral margin of the mandible has a slight excision, but lacks a ventral tooth; the head below the eyes widens towards the mandibular insertions; the first metasoma segment is sessile with the second segment; and the pygidium is longitudinally striate and granulate between the striae; the eyes are larger than the distance from the posterior margin of the eye to the vertex of the head (the eye is from 1.2 to 1.4 times as big as the length from the margin of the eye to the vertex of the head); and the apical margins of the tergites have dense fringes of white plumose setae.

Distribution.—This species is widespread in the Mojave and Sonoran deserts. It is also present in the Great Basin Desert, the Colorado Plateau and the Snake River Plain.

Material Examined. **MEXICO: Baja California** **Sur:** Guerrero Negro, sand dunes 8 km N, 2 ♂, 8–9.Sep.1977, R.R. Snelling (LACM). **USA:** **Arizona:** *Cochise Co.:* Chiricahua Mtns., S. Cave Creek Cyn., 3 ♂ 11.Sep.1979, Knowlton, Hanson (EMUS); Huachuca Mtns., Ramsey Canyon, 1 ♂, 29.May.1964, B.F. Sternitzky (PMNH); *Sierra Vista,* 1 ♂, 16.Jun.1964, B.F. Sternitzky (PMNH); *Santa Cruz Co.:* Sycamore Cyn., Ruby Road, 2 ♂, 9.Sep.1979, Knowlton, Hanson (EMUS). **California:** *Imperial Co.:* Algodones Dunes: Niland-Glamis Road, 7.4 km NW Glamis, 1 ♂, 1–2.Jun.2008, Museum Survey Team (UCDC); *Inyo Co.:* Independence, 2 mi E, 3 ♂, 2.Jul.1968 (CSCA); *Inyo Mtns,* 12 mi E Big Pine, 1 ♀, 21.Aug.1982, D. Giuliani (EMUS); *White Mtns.,* Grand View Camp, 1 ♂, 24.Jul.1982, N.J. Smith (UCDC); *Riverside Co.:* Corn Springs, 5 mi N Desert Center, 10 ♂, 21.May.2004, 18 ♂, 24.Jun.2004, K.A. Williams (KAWC); Deep Canyon Desert Research Center, 1 ♂, 2–5.Jun.2002, M.E. Irwin and F.D. Parker (EMUS); Wiley Well, 1 ♂ 12.Oct.1941, G.I. Virlett (LACM). **Idaho:** *Owyhee Co.:* Bruneau Dunes State Park, 1 ♂, 19.Jun.2008, J.S. Wilson and L.E. Wilson (EMUS). **Nevada,** *Clark Co.:* Corn Creek, 1 ♂, 18.Jun.1965, T.W. and W.T. Davies (PMNH); Willow Creek, 1 ♂, 14.Aug.1972, G.M. Nishida (NVDA); *Douglas Co.:* Pine Nut Creek, 1 ♂, 7.Aug.1972, G.M. Nishida (NVDA); *Esmeralda Co.:* Middle Creek, 1 ♂, 22.Jul.1971, G.M. Nishida (NVDA); *Lincoln Co.:* Beaver Dam St Prk, 1 ♂, 11.Aug.1971, D.F. Zoller (NVDA); Modena summit, 1 ♂, 28.Jul.1976, R.C. Bechtel, J.B. Knight and D.F. Zoller (NVDA); Oak springs summit, 8 ♂, 6–10.Aug.1974, G.M. Nishida and D.F. Zoller (NVDA); Pioche, 2 ♂, 6.Aug.1981, P.C. Bechtel (NVDA); *Lyon Co.:* Yerington, 3 mi E, 1 ♂, 8.Aug.1973, G.M. Nishida (NVDA); *Mineral Co.:* Whisky Flat, 1 ♂, 11.Jul.1979, R.C. Bechtel and R.L. Bradley (NVDA); *Nye Co.:* Beatty, 2.3 mi NW, 1 ♂, 15.May.1971 (CSCA); Nevada Test Site, 2 ♀, 22.Jul.1967, 1 ♀, 14.Jul.1967, 1 ♀ 31.Jul.1967, 2 ♀ 18.Aug.1967 (EMUS); Nellis AFB, Groom Lake Rd, 9.2 mi N, 1 ♀, 14.Jul.1967, 1 ♀, 24.Jul.1967 (EMUS); Nellis AFB, Groom Lake Rd, 11 mi N, 1 ♀, 8.Jul.1967, 1 ♀, 17.Jul.1967 (EMUS); Peavine Cyn, 1 ♂, 11.Aug.1967, C.D. Cooney (NVDA); *Storey Co.:* Virginia City highlands, 1 ♂, 11.Aug.1984, J.B. Knight (NVDA); *White Pine Co.:* Mt Hamilton, 1 ♀, 21.Jun.1974, L.V. Barclay (NVDA). **New Mexico:** *San Juan Co.:* Farm-

ington, 3 mi S, 5 ♂, 10–11.Jun.2007, J.S. Wilson and L.E. Wilson (EMUS). **Utah:** *Emery Co.:* Gilson's Butte, 7 ♂, 20.Aug.2001, M.E. Irwin, F.D. Parker (EMUS); Goblin Valley State Preserve, 2 mi N, 18 ♂, 13 ♀ 25.Aug.1980, A.S. Menke F.D. Parker and K.A. Menke (EMUS); Hanksville, 16 mi N, 14 ♂, 1 ♀, 18.Sep.1980, Hanson and Knowlton (EMUS); Huntington, 2 ♂, 21.Jul.1940, F.C. Harmston (EMUS); Little Flat Top, 3 ♂, 22–26.Jul.2001, M.E. Irwin, F.D. Parker (EMUS); Little Gilson Butte: 2 mi W, 49 ♂, 7 ♀, 15–17.Sep.1980, Griswold, Parker and Veirs (EMUS); 4 ♂, 20–23.Jul.1981, Griswold, Parker and Veirs (EMUS); San Rafael Desert, nr Goblin Valley, 4 ♂, Sep.1980, G.E. Bohart (EMUS); Wild Horse Creek, N Goblin Valley, 6 ♂, 16–17.Sep.1980; 3 ♂, 21–23.Jul.1980, Griswold and Parker (EMUS); *Garfield Co.:* Buckskin spring, N Goblin Valley, 23 ♂, 2.Aug.1997, M.J. Wasbauer (UCDC); Escalante, 37 km SE, 29 ♂, 11.Aug.1997, M.J. Wasbauer (UCDC); Long Canyon, 4 ♂, 5–19.Jul.2003, H. Ikerd (EMUS); Shootering Cyn., 1 ♂, 1.Jul.1978, D. Vogt (EMUS); Starr Springs, 1 ♂, 27.Aug.1971, D.F.H. (EMUS); Wild Horse Creek, N Goblin Valley, 7 ♂, 5.Aug.1997, M.J. Wasbauer (UCDC); *Grand Co.:* Moab, 13 mi W, 1 ♂, 26.Aug.1971 (EMUS); *San Juan Co.:* Lime creek, 1 ♂, 13.Jul.1967, S. Waldron (EMUS); *Uinta Co.:* Bonanza, SW, 1 ♂, 30.Jul.1978, G.E. Bohart; 2 ♂, 3.Aug.1981, 2 ♂, 11.Aug.1981, 1 ♂, 28.Aug.1981, M. Schwartz and R. Miller (EMUS); Vernal, 19.Jul.1941, 3 ♂, G.F. Knowlton (EMUS); White River, 3 mi S Bonanza, 3 ♂, 10.Aug.1964, B and C Durden (PMNH). *Washington Co.:* Leeds, 1 ♀, 13.Jun.1961, D.W. Davis (EMUS); Leeds, Oak Grove CG, 1 ♀, 8.Jun.1964, D.W. Davis (EMUS); *Wayne Co.:* Hanksville, 14 mi S, 5 ♂, 25.Jul.1978, Hardy and Andrews (CSCA).

Remarks.—There is a wide array of integumental coloration in this species. Specimens range from nearly black integument to a more reddish-brown color characteristic of most nocturnal mutillids. Female integumental coloration has a similar range as the males. The setal coloration rarely varies among *S. mendica* specimens. Some individuals have pale orange setae on their mesosoma, but the majority has entirely white setae. All specimens have dense fringes of white

plumose setae on the apical margins of the tergites. Female *S. mendica* specimens often appear less setose than females of *S. unicolor*.

Sphaerophthalma angulifera Schuster

Sphaerophthalma (*Photopsis*) *angulifera* Schuster, 1958. Ent. Amer. 37: 32. Male. Holotype data: California, Kern Co., Bakersfield (CASC).

Diagnosis of male.—The male of this species can be recognized by having mandibles that are weakly excised ventrally with a distinct angulate basal tooth and an apex that is tridentate and oblique, but most importantly the dorsal carina of the mandible is angulate at the midpoint of the mandible coinciding with the ventral tooth (Fig. 8), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternite has a distinct felt line, and the pygidium is granulate. The genitalia are similar to *S. unicolor* (Fig. 3). The cuspis is a uniform diameter from the base to the apex (Fig. 3).

Diagnosis of female.—The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with moderately dense erect pale golden brachyplumose setae that do not obscure the integument; the ventral margin of the mandible has a slight excision followed by a distinct angulate tooth; the head below the eyes widens towards the mandibular insertions; the first metasomal segment is sessile with the second; the pygidium is granulate; and the apical margins of the tergites have dense fringes of white plumose setae.

Description of female: Coloration and setal pattern. Body testaceous. Legs and flagellum lighter. Moderately dense pale golden brachyplumose setae throughout; integumental sculpture visible. Metasomal segments with dense fringe of white plumose setae. Legs with white brachyplumose setae.

Head. Head rounded posteriorly, not as wide as mesosoma, moderately punctate.

Width of face at mandibular base wider than width immediately ventral to eyes. Eye ovate, distance from posterior mandibular articulation $\sim 2.5\times$ visible length of pedicel. Clypeus protruding anteriorly, posteromedially produced into low triangular tubercle. Antennal scrobe with indistinct dorsal carina. Antennal tubercle glabrous. Flagellomere I $\sim 1.3\times$ length of pedicel. Flagellomeres II–III $\sim 1.0\text{--}1.1\times$ length of pedicel. Mandible bidentate apically. Ventral mandibular margin with slight angulate basal tooth; dorsal margin with incomplete carina ending at basal third of mandible, not produced apically as tubercle. Genal carina absent.

Mesosoma. Mesosoma slightly wider anteriorly than posteriorly, slightly longer than broad. Mesosoma coarsely punctate on dorsum. Propleuron anteriorly, mesopleuron medially running vertically, and extreme ventral region of propodeal side punctate. Humeral angle dentate. Scutellar scale absent. Mesosternum with low transverse tubercle present medially just anterior to mesocoxa. Metasternum tridentate. Propodeum with distinct dorsal and vertical faces; lateral face impunctate.

Metasoma. Segment 1 distinctly sessile with segment 2. T1 with small sparse punctures. Tergite 2 with sparse shallow punctures. T2 with felt line; length $0.2\times$ length of tergite. T3–5 shagreened. T6 with distinct pygidial area defined by weak carinae; surface strongly densely granulate. S2–5 with punctuation similar to tergites.

Length. $\sim 6.4\text{--}11$ mm.

Distribution.—This species is found in the Mojave and Western Sonoran deserts.

Material examined.—USA: California: Kern Co.: Maricopa, 5 mi SW, 3 ♂, 16.Sep.2004, EE & KA Williams (KAWC); San Bernardino Co.: Lucerne Valley, 10 mi SE, 3 ♂, 16.Sep.2004, EE & KA Williams (KAWC); Inyo Co.: Olancha, 3 mi NE, Sand Dunes, 3.Jul.2005, 1 ♂, KA Williams (KAWC); Olancha, 4 mi NE, Dirty Socks Hot Springs, 3.Jul.2005, KA Williams (KAWC); Nevada: Nye Co.: Mercury, 1 ♂, 4.May.1961, 1 ♀, 8.May.1961, 1 ♀, 19.May.1961, 1 ♀, 1.Jun.1961,

1 ♂, 19.Jun.1961, 1 ♀, 20.Jun.1961, 1 ♂, 21.Jun.1961, 1 ♀, 22.Jun.1961, 1 ♀, 6.Jul.1961, 1 ♂, 21.Jul.1961 (BYUC). Utah: Washington Co.: Leeds Canyon, 1 ♂, 17.Jul.1980, Hanson, Knowlton & Clemons (EMUS); Zion National Park, 1 ♂, 23.Jul.1978, 1 ♂, 22.Sep.1978, Gafney (EMUS).

Remarks.—While *S. angulifera* is morphologically similar to *S. unicolor* and *S. mendica*, it can easily be differentiated from these two species. There is little variation in the integumental coloration of *S. angulifera*, most specimens are a yellowish-brown, similar to the majority of nocturnal mutilids. No differences were found in setal coloration of this species, all specimens are clothed with orange setae on the apical margins of the tergites.

The sex association is based on similarities of the female to that of *S. mendica* and distributional data. Ferguson (1967) collected both *S. mendica* and *S. angulifera* at the Nevada Test Site. After studying the morphology of an unknown set of females, he decided that they appeared to be closely related to *S. mendica*. The only closely related species at the Test Site was *S. angulifera*, which happened to be known only from the male. He concluded that these two sexes must be conspecific, but never published this information. We agree with his conclusions.

DISCUSSION

Molecular tools are becoming increasingly important in deciphering cryptic or morphologically challenging species complexes (Pilgrim and Pitts 2006; von Dohlen et al. 2006; Pitts et al. 2007; Wilson and Pitts 2008). Our analysis of *S. unicolor* uncovered the existence of two sister species, *S. angulifera* and *S. mendica*, the latter being previously unrecognized. After a thorough morphological analysis of these species, multiple traits were discovered that support the molecular data.

While relatively large genetic distances separate these species (Table 1), the intra-species variation differs between species. Populations of *S. unicolor*, for example, all

have nearly identical ITS1 and ITS2 sequences, being separated only by small genetic distances (Table 1). This suggests that there is gene flow between populations of *S. unicolor*. Populations of *S. mendica*, however, are separated by larger genetic distances (Table 1), which suggests reduced or no gene flow is occurring between some populations. Genetic distances among populations of *S. mendica* that exhibit the same color morph are also somewhat large (Reddish-brown form: 0.3% for ITS1 and 0.7% for ITS2; Melanistic form: 0.3% for ITS1 and 0.4% for ITS2). These distances are slightly lower than the genetic distances between the Reddish-brown form and the Melanistic form of *S. mendica* (0.6%–1.1% for ITS1 and 0.5–0.9% for ITS2). This suggests that the two color morphs rarely, if ever, interbreed. But, because only few individuals were analyzed, more data are needed to determine the amount of gene flow between these color forms. It is likely that additional specimens, from a broader geographic region, could show that there is no significant genetic difference between these two forms. Because of the low genetic distance, coupled with the lack of morphological differentiation, between color morphs of *S. mendica*, we feel that, until more data can be gathered that suggests otherwise, these color forms should be considered the same species.

Ferguson (1967) suggested that the Melanistic form of *S. mendica* was geographically isolated from the Reddish-brown form by elevation, with the darker form being found only above 5,500 ft. We found this not to be the case. We have collected the Melanistic form of *S. mendica* at elevations ranging from 2,500 ft in southern Idaho, to 6,000 ft in southern Utah. Also, we have collected the Reddish-brown form at elevations ranging from 1,600 ft in the Sonoran Desert to 6,600 ft in southern Utah. While there does seem to be a phylogenetic split between these color forms (Fig. 1), it is not easily explained by elevation. Differences in integumental col-

oration do not appear to suggest species-level differences in *S. mendica*. It is possible that the differences seen in this species are due to humidity differences during development as Ferguson (1962) suggested, but more research must be done before this conclusion can be made.

Setal coloration in some mutillid wasps (e.g., *Dasymutilla*) is variable within a single species and is, therefore, not always reliable to diagnose species (Pilgrim et al. 2009). The differences in setal coloration between *S. mendica* and *S. unicolor* are, however, consistent and useful in diagnosing these two species. Differences in color, without any additional structural differences, should rarely be used to differentiate between species. Researchers must use caution when describing new species based solely on differences in color. When these color differences are also supported by structural and/or genetic differences, color can be a useful and easy way to diagnose species.

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